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Description of a new cave-dwelling species of *Claea* (Teleostei, Cypriniformes, Nemacheilidae) from the Yangtze River basin in Sichuan, southern China

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Abstract

The first obligatory troglobitic *Claea* species, *Claea scet*, is described from a subterranean river in a cave connected to the Yangtze River in Hulu Town, Shawan District, Leshan City, Sichuan Province, southern China. *C. scet* differs from all congeners by the following combination of characters: Body pale without pigmentation; eye vestigial, diameter of eye 3.8–5.9% SL; short anal fin, anal fin height 7.0–8.4% SL. Molecular phylogenetic analysis supported the validity of the new species and revealed a close relationship between *Claea* and hypogean *Triplophysa* species.

Key Words

Cavefish, *Claea*, morphology, Nemacheilidae, phylogeny

Introduction

The genus *Claea*, a group featuring small benthic nemacheilid fishes adapted to torrential habitats, is characterized by the presence of a processus dentiformis on the median portion of the upper jaw, the absence of an adipose crest between the dorsal fin and caudal fin base, a scaleless body, the lack of a supra-pelvic flap, and the absence of marked sexual dimorphism. This genus is widely distributed in the upper Yangtze River basin in China (Kottelat 2012). The genus was first established by Sauvage (1874) based on the type species *Oreias dabryi* (now *C. dabryi*), described from a single specimen collected in Dengchigou, Baoxing County, Ya'an City, Sichuan Province, China (Kottelat 2012). The taxonomic validity of *Oreias* has been historically contentious due to insufficient original descriptions and ambiguous type locality information. Consequently, *O. dabryi* was subsequently reclassified into *Barbatula* and *Nemachilus* in later studies, reflecting uncertainties in key intergeneric diagnostic traits (Nichols 1944; Cao and Wu 1962). Bănărescu and Nalbant (1976) re-examined and redescribed the type specimen of *O. dabryi* and described two additional species, *O. furcatus* from Sichuan Province and *O. crassipedunculatus* from Yunnan Province, China, based on preserved specimens. Later, a new subspecies, *Oreias dabryi nanpanjiangensis*, was described from the Nanpanjiang River, a tributary of the Pearl River (Zhu and Cao 1988). Zhu (1989) proposed that *Oreias* was a junior synonym of *Schistura*, with *O. furcatus* and *O. crassipedunculatus* synonymized under *S. dabryi*.

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However, Chu and Chen (1990) reinstated the validity of *Oreias* and reclassified *Oreias dabryi nanpanjiangensis* as a species of *Triplophysa*, citing the presence of sexual dimorphism and the absence of a prominent median upper jaw protrusion, which are diagnostic features of *Triplophysa*. Subsequent studies accepted the validity of *Oreias*, and two new species were described from the Yangtze River basin: *O. dabryi microphthalmus* (= *Claea microphthalmus*) and *O. niulanjiangensis* (Ding and Deng 1990; Wu and Wu 1992; Liao et al. 1997; Chen 1998; Chen et al. 2006; Zhang and Zhao 2016; Zhang et al. 2019; Du et al. 2021; Guo 2021). Outside of China, five species have been reported in Vietnamese literature (Nguyen 2005; Hoa et al. 2012), including two from the Lixiangjiang River, a tributary of the Red River (*O. sonlaensis* and *O. trilineatus*), and three from the Vietnamese Mekong (*O. hoai*, *O. lineatus*, and *O. punctatus*). The generic name *Oreias* Sauvage, 1874, was noted as a junior homonym of *Oreias* Kaup, 1829 (Aves) and *Oreias* Temminck, 1838 (Aves), prompting the proposal of *Claea* as a replacement name (Kottelat 2011). Kottelat (2012) further revised the genus, reclassifying *C. microphthalmus* into *Triplophysa* and assigning all Vietnamese species to *Schistura*, thereby restricting the genus *Claea* to the upper Yangtze River basin in China. Zhang et al. (2024) recently revised *Claea*, transferring *C. niulanjiangensis* to *Triplophysa* and reclassifying *T. wulongensis* from the Wujiang River as *C. wulongensis* based on the absence of secondary sexual characteristics and the presence of a prominent processus dentiformis. Additionally, they described a new species, *C. minibarba*, from the Shennongxi and Qingjiang River, tributaries of the upper Yangtze River in Hubei Province, China. Currently, *Claea* comprises three recognized species: *C. dabryi*, *C. minibarba*, and *C. wulongensis*.

The extensive karst mountain regions in southwestern China, characterized by numerous limestone caves and subterranean river systems, provide habitats for a diverse array of cave-adapted fish species, including members of the nemacheilid genera *Eoemacheilus*, *Guinemachilus*, *Karstsinnectes*, *Oreonectes*, *Paranemacheilus*, *Triplophysa*, *Troglonectes*, and *Yunnanilus* (Lan et al. 2013; Liu et al. 2017; Wu et al. 2018; Ma et al. 2019; Du et al. 2023; Luo et al. 2023a). Many of these species exhibit obligate troglobitic adaptations, including reduced eyes, elongated fins, and depigmentation. However, members of *Claea* are typically epigean, with no prior records from subterranean environments except for *C. wulongensis*, which lacks definitive troglobitic features (Chen et al. 2021). In May 2023, during a cave survey in Taojin Cave, part of the Dadu River basin (a tributary of the upper Yangtze River) in Sichuan Province, China, specimens of an obligate troglobitic nemacheilid fish were collected. Comprehensive morphological and phylogenetic analyses confirmed these specimens as the first obligatory troglobitic species of *Claea*, herein described as *Claea scet* sp. nov.

Materials and methods

Sample collection

A total of 16 specimens were collected from Taojin Cave, located in Shiqianggou, Hulu Town, Shawan District, Leshan City, Sichuan Province, China, within the Dadu River basin, during May 2023 and June 2024. Specimens were captured using hand-nets and subsequently transferred to an aquarium for behavioral observation over several days. Following the observation period, individuals were euthanized using eugenol in accordance with ethical guidelines. Tissue samples from the right fin (n = 5) were excised and preserved in 95% ethanol for molecular analysis, with storage maintained at –20 °C to ensure DNA integrity. Whole specimens were fixed in 5% formaldehyde for 5–7 days and then transferred to 75% ethanol for long-term preservation. All collected specimens were cataloged and deposited in the Museum of Aquatic Organisms at the Institute of Hydrobiology, Chinese Academy of Sciences (IHB). The handling and experimental procedures involving these specimens adhered strictly to the ethical standards outlined in the Chinese Laboratory Animal Welfare and Ethics guidelines (GB/T 35892–2018).

Morphometric data acquiring

Morphometric data were collected using digital calipers interfaced directly with a computer, ensuring precision to the nearest 0.1 mm. Measurements and meristic counts (Table 2) were conducted on the left side of each specimen, following the standardized methodology outlined by Rainboth and Kottelat (1991). All linear measurements are expressed as proportions of either standard length (SL) or lateral head length (HL). The internostril width was defined as the linear distance between the anterior margins of the nostrils. Fin ray counts were performed under a ZEISS Stemi 508 stereomicroscope to ensure accuracy. For anatomical analysis, one specimen of each species was dissected to examine the morphology of the intestine and the structural configuration of the air bladder chambers. Vertebral counts (n = 1) were obtained from microcomputed tomography (CT) images acquired using a Siemens Somatom Definition X-ray machine, with three-dimensional reconstructions generated using CTvox software.

DNA extraction, amplification, sequencing, and phylogenetic analysis

Total genomic DNA was extracted from pelvic fin tissue using the rapid salt-extraction protocol (Aljanabi and Martinez 1997). The mitochondrial Cytochrome *b* gene (Cyt *b*) and Cytochrome oxidase subunit 1 (*CO*I) gene were amplified and sequenced for two individuals (IHB 202305300003 & IHB 202305300005), following the methodologies described by He and Chen

(2009). Electropherograms were manually inspected for quality using Chromas 2.22 (Technelysium Pty Ltd), and sequence alignments were performed using Clustal X 2.0 (Larkin et al. 2007).

A total of 145 complete mitochondrial genomes or sequences of the Cyt *b* and *CO*I genes from genera *Claea*, *Triplophysa*, *Troglonectes*, *Traccatichthys*, *Schistura*, *Oreonectes*, *Lefua*, *Karstsinnectes*, *Hedinichthys*, and *Barbatula* within the family Nemacheilidae were retrieved from the NCBI database. These sequences were utilized to reconstruct molecular phylogenetic relationships. Corresponding GenBank accession numbers are provided in Table 1.

Phylogenetic trees were constructed using both maximum likelihood (ML) and Bayesian inference (BI) methods. The concatenated dataset included the Cyt *b* and *CO*I genes, as well as complete mitochondrial genome sequences, excluding the D-loop region. Cyt *b* and *CO*I fragements were manually selected from complete mitochondrial genome sequences according to annotations from GenBank. Sequences were aligned in MAFFT v.7.245 (Katoh and Standley 2013) and manually examined in AliView (Larsson 2014) to ensure the correct reading frame. Thirty-four species from the family Cobitidae were designated as outgroups. The optimal nucleotide substitution model was determined using jModelTest 2.1.4 (Darriba et al. 2012), with the best-fit model (GTR + G + I) selected based on Akaike's Information Criterion (AIC) among 88 candidate models. ML analysis was conducted in RAxML 8.2.10 (Stamatakis 2014) under the GTRGAMMAIX model, with 2000 bootstrap replicates to assess node support. BI analysis was performed using MrBayes 3.2.6 (Ronquist et al. 2012), with two independent runs of two million generations each and four Markov chain Monte Carlo (MCMC) chains. Convergence of the BI analysis was evaluated based on the average standard deviation of split frequencies. Resulting phylogenetic trees were visualized and annotated using FigTree 1.4.4 (Rambaut 2018). Additionally, mean pairwise *p*-distances (number of substitutions per site) among haplotypes within the genus *Claea* were calculated based on the Cyt *b* gene using MEGA11 software (Tamura et al. 2021).

Table 1. GenBank accession numbers of loach species used in the phylogenetic analysis.

GenBank accession numbers	Species	Family	Genes
AB242161	*Acantopsis choirorhynchos*	Cobitidae	complete mitochondrial genome
NC_027663	*Cobitis biwae*	Cobitidae	complete mitochondrial genome
EU333980	*Cobitis choii*	Cobitidae	complete mitochondrial genome
EU656112	*Cobitis choii*	Cobitidae	complete mitochondrial genome
KF926686	*Cobitis elongatoides*	Cobitidae	complete mitochondrial genome
KF908768	*Cobitis granoei*	Cobitidae	complete mitochondrial genome
MZ339224	*Cobitis hankugensis*	Cobitidae	complete mitochondrial genome
MN841275	*Cobitis hankugensis*	Cobitidae	complete mitochondrial genome
MN756662	*Cobitis hugowolfeldi*	Cobitidae	complete mitochondrial genome
MT259034	*Cobitis macrostigma*	Cobitidae	complete mitochondrial genome
MK156771	*Cobitis macrostigma*	Cobitidae	complete mitochondrial genome
NC_029441	*Cobitis matsubarae*	Cobitidae	complete mitochondrial genome
MH349461	*Cobitis nalbanti*	Cobitidae	complete mitochondrial genome
MZ707538	*Cobitis nigrolinea*	Cobitidae	complete mitochondrial genome
AY526868	*Cobitis sinensis*	Cobitidae	complete mitochondrial genome
AP010782	*Cobitis striata*	Cobitidae	complete mitochondrial genome
AB054125	*Cobitis striata*	Cobitidae	complete mitochondrial genome
AP009306	*Cobitis takatsuensis*	Cobitidae	complete mitochondrial genome
OQ645452	*Cobitis tetralineata*	Cobitidae	complete mitochondrial genome
OP651767	*Lepidocephalichthys berdmorei*	Cobitidae	complete mitochondrial genome
DQ026434	*Misgurnus anguillicaudatus*	Cobitidae	complete mitochondrial genome
PP932689	*Misgurnus anguillicaudatus*	Cobitidae	complete mitochondrial genome
KF562047	*Misgurnus bipartitus*	Cobitidae	complete mitochondrial genome
MF579258	*Misgurnus mizolepis*	Cobitidae	complete mitochondrial genome
KF386025	*Misgurnus mohoity*	Cobitidae	complete mitochondrial genome
AB242171	*Misgurnus nikolskyi*	Cobitidae	complete mitochondrial genome
AB242168	*Pangio anguillaris*	Cobitidae	complete mitochondrial genome
NC_033958	*Paracanthocobitis botia*	Cobitidae	complete mitochondrial genome
NC_033959	*Paracanthocobitis zonalternans*	Cobitidae	complete mitochondrial genome
KJ027397	*Paramisgurnus dabryanus*	Cobitidae	complete mitochondrial genome
KF771003	*Paramisgurnus dabryanus*	Cobitidae	complete mitochondrial genome
ON116497	*Paranemachilus genilepis*	Cobitidae	complete mitochondrial genome
ON116499	*Paranemachilus jinxiensis*	Cobitidae	complete mitochondrial genome
ON116530	*Paranemachilus zhengbaoshani*	Cobitidae	complete mitochondrial genome
KT906089	*Claea dabryi*	Nemacheilidae	complete mitochondrial genome
MG238214/MG238118	*Claea dabryi*	Nemacheilidae	Cyt *b*, *CO*I
MG238216/MG238120	*Claea dabryi*	Nemacheilidae	Cyt *b*, *CO*I
PQ860813/PQ860770	*Claea scet* sp. nov.	Nemacheilidae	Cyt *b*, *CO*I
PQ860814/PQ860771	*Claea scet* sp. nov.	Nemacheilidae	Cyt *b*, *CO*I
OP750011	*Claea minibarba*	Nemacheilidae	Cyt *b*

GenBank accession numbers	Species	Family	Genes
OP750012	*Claea minibarba*	Nemacheilidae	Cyt *b*
OP750013	*Claea minibarba*	Nemacheilidae	Cyt *b*
OP750014	*Claea minibarba*	Nemacheilidae	Cyt *b*
OP750015	*Claea minibarba*	Nemacheilidae	Cyt *b*
KP715096	*Barbatula barbatula*	Nemacheilidae	complete mitochondrial genome
CM074126	*Barbatula barbatula*	Nemacheilidae	complete mitochondrial genome
PQ354418	*Barbatula barbatula*	Nemacheilidae	complete mitochondrial genome
KT192057	*Barbatula labiata*	Nemacheilidae	complete mitochondrial genome
KF574248	*Barbatula nuda*	Nemacheilidae	complete mitochondrial genome
MW288293	*Barbatula quignardi*	Nemacheilidae	complete mitochondrial genome
KT259193	*Barbatula* sp.	Nemacheilidae	complete mitochondrial genome
MK900633	*Barbatula toni*	Nemacheilidae	complete mitochondrial genome
AB242162	*Barbatula toni*	Nemacheilidae	complete mitochondrial genome
KM405199	*Barbatula toni*	Nemacheilidae	complete mitochondrial genome
KM017732	*Hedinichthys potanini*	Nemacheilidae	complete mitochondrial genome
JX144893	*Hedinichthys variegatus*	Nemacheilidae	complete mitochondrial genome
MN821008	*Hedinichthys yarkandensis*	Nemacheilidae	complete mitochondrial genome
KP050360	*Hedinichthys yarkandensis*	Nemacheilidae	complete mitochondrial genome
KT224367	*Hedinichthys yarkandensis*	Nemacheilidae	complete mitochondrial genome
KT192439	*Hedinichthys yarkandensis*	Nemacheilidae	complete mitochondrial genome
OP554813	*Hedinichthys yarkandensis*	Nemacheilidae	complete mitochondrial genome
KX447641	*Hedinichthys yarkandensis*	Nemacheilidae	complete mitochondrial genome
ON116515	*Karstsinnectes acridorsalis*	Nemacheilidae	complete mitochondrial genome
ON116506	*Karstsinnectes anophthalmus*	Nemacheilidae	complete mitochondrial genome
ON116531	*Karstsinnectes parvus*	Nemacheilidae	complete mitochondrial genome
ON116520	*Karstsinnectes parvus*	Nemacheilidae	complete mitochondrial genome
KT943751	*Lefua costata*	Nemacheilidae	complete mitochondrial genome
AB054126	*Lefua echigonia*	Nemacheilidae	complete mitochondrial genome
ON116504	*Micronemacheilus bailianensis*	Nemacheilidae	complete mitochondrial genome
NC_033960	*Micronemacheilus cruciatus*	Nemacheilidae	complete mitochondrial genome
ON116508	*Micronemacheilus longibarbatus*	Nemacheilidae	complete mitochondrial genome
MK387705	*Micronemacheilus pulcherrimus*	Nemacheilidae	complete mitochondrial genome
MZ853161	*Micronemacheilus pulcherrimus*	Nemacheilidae	complete mitochondrial genome
ON116507	*Oreonectes guananensis*	Nemacheilidae	complete mitochondrial genome
ON116495	*Oreonectes luochengensis*	Nemacheilidae	complete mitochondrial genome
ON116496	*Oreonectes platycephalus*	Nemacheilidae	complete mitochondrial genome
MW043722	*Oreonectes polystigmus*	Nemacheilidae	complete mitochondrial genome
AB242172	*Schistura balteata*	Nemacheilidae	complete mitochondrial genome
PP212943	*Schistura callichromu*	Nemacheilidae	complete mitochondrial genome
KY404236	*Schistura fasciolata*	Nemacheilidae	complete mitochondrial genome
MK361215	*Schistura incerta*	Nemacheilidae	complete mitochondrial genome
KU380330	*Schistura scaturigina*	Nemacheilidae	complete mitochondrial genome
PP114298	*Schistura yingjiangensis*	Nemacheilidae	complete mitochondrial genome
ON116516	*Traccatichthys pulcher*	Nemacheilidae	complete mitochondrial genome
ON116518	*Traccatichthys zispi*	Nemacheilidae	complete mitochondrial genome
KT213584	*Triplophysa aliensis*	Nemacheilidae	complete mitochondrial genome
KT213585	*Triplophysa alticeps*	Nemacheilidae	complete mitochondrial genome
MZ325251	*Triplophysa angeli*	Nemacheilidae	complete mitochondrial genome
KJ739868	*Triplophysa anterodorsalis*	Nemacheilidae	complete mitochondrial genome
MT992550	*Triplophysa baotianensis*	Nemacheilidae	complete mitochondrial genome
JQ686729	*Triplophysa bleekeri*	Nemacheilidae	complete mitochondrial genome
JX135578	*Triplophysa bleekeri*	Nemacheilidae	complete mitochondrial genome
MZ958819	*Triplophysa bombifrons*	Nemacheilidae	complete mitochondrial genome
KR052018	*Triplophysa bombifrons*	Nemacheilidae	complete mitochondrial genome
KT213588	*Triplophysa brevicauda*	Nemacheilidae	complete mitochondrial genome
KT213589	*Triplophysa chondrostoma*	Nemacheilidae	complete mitochondrial genome
KY945352	*Triplophysa cuneicephala*	Nemacheilidae	complete mitochondrial genome
OR857527	*Triplophysa dalaica*	Nemacheilidae	complete mitochondrial genome
KY945353	*Triplophysa dalaica*	Nemacheilidae	complete mitochondrial genome
KT213590	*Triplophysa dalaica*	Nemacheilidae	complete mitochondrial genome
OR857526	*Triplophysa dalaica*	Nemacheilidae	complete mitochondrial genome
OR857525	*Triplophysa dalaica*	Nemacheilidae	complete mitochondrial genome
OR857524	*Triplophysa dalaica*	Nemacheilidae	complete mitochondrial genome
OR857523	*Triplophysa dalaica*	Nemacheilidae	complete mitochondrial genome
KT213591	*Triplophysa dorsalis*	Nemacheilidae	complete mitochondrial genome
KT241024	*Triplophysa dorsalis*	Nemacheilidae	complete mitochondrial genome
PP455386	*Triplophysa erythraea*	Nemacheilidae	complete mitochondrial genome
PQ040451	*Triplophysa erythraea*	Nemacheilidae	complete mitochondrial genome
OQ998929	*Triplophysa fengshanensis*	Nemacheilidae	complete mitochondrial genome
PP114297	*Triplophysa grahami*	Nemacheilidae	complete mitochondrial genome
KT213592	*Triplophysa hsutschouensis*	Nemacheilidae	complete mitochondrial genome

GenBank accession numbers	Species	Family	Genes
OQ603602	*Triplophysa jianchuanensis*	Nemacheilidae	complete mitochondrial genome
ON116521	*Triplophysa langpingensis*	Nemacheilidae	complete mitochondrial genome
KT966735	*Triplophysa lixianensis*	Nemacheilidae	complete mitochondrial genome
OQ998928	*Triplophysa longipectoralis*	Nemacheilidae	complete mitochondrial genome
OQ998931	*Triplophysa longliensis*	Nemacheilidae	complete mitochondrial genome
KT213594	*Triplophysa markehenensis*	Nemacheilidae	complete mitochondrial genome
PP979136	*Triplophysa microphthalma*	Nemacheilidae	complete mitochondrial genome
KT213595	*Triplophysa microps*	Nemacheilidae	complete mitochondrial genome
KT213596	*Triplophysa minxianensis*	Nemacheilidae	complete mitochondrial genome
KT213597	*Triplophysa moquensis*	Nemacheilidae	complete mitochondrial genome
OQ998932	*Triplophysa nandanensis*	Nemacheilidae	complete mitochondrial genome
OQ274895	*Triplophysa nanpanjiangensis*	Nemacheilidae	complete mitochondrial genome
OQ992507	*Triplophysa nasobarbatula*	Nemacheilidae	complete mitochondrial genome
ON116529	*Triplophysa nasobarbatula*	Nemacheilidae	complete mitochondrial genome
MT361978	*Triplophysa nasobarbatula*	Nemacheilidae	complete mitochondrial genome
KT213598	*Triplophysa nujiangensa*	Nemacheilidae	complete mitochondrial genome
KT213599	*Triplophysa orientalis*	Nemacheilidae	complete mitochondrial genome
KJ631323	*Triplophysa orientalis*	Nemacheilidae	complete mitochondrial genome
KT213600	*Triplophysa pappenheimi*	Nemacheilidae	complete mitochondrial genome
KY419201	*Triplophysa pappenheimi*	Nemacheilidae	complete mitochondrial genome
KT213601	*Triplophysa pseudostenura*	Nemacheilidae	complete mitochondrial genome
KM396312	*Triplophysa robusta*	Nemacheilidae	complete mitochondrial genome
KM406486	*Triplophysa robusta*	Nemacheilidae	complete mitochondrial genome
JF268621	*Triplophysa rosa*	Nemacheilidae	complete mitochondrial genome
MW582822	*Triplophysa sanduensis*	Nemacheilidae	complete mitochondrial genome
KT213602	*Triplophysa scleroptera*	Nemacheilidae	complete mitochondrial genome
KY851112	*Triplophysa sellaefer*	Nemacheilidae	complete mitochondrial genome
KT213603	*Triplophysa siluroides*	Nemacheilidae	complete mitochondrial genome
KJ781206	*Triplophysa siluroides*	Nemacheilidae	complete mitochondrial genome
KT213587	*Triplophysa* sp.	Nemacheilidae	complete mitochondrial genome
KT259195	*Triplophysa* sp.	Nemacheilidae	complete mitochondrial genome
KT456271	*Triplophysa* sp.	Nemacheilidae	complete mitochondrial genome
KT213586	*Triplophysa* sp.	Nemacheilidae	complete mitochondrial genome
ON116519	*Triplophysa* sp.	Nemacheilidae	complete mitochondrial genome
KX376478	*Triplophysa* sp.	Nemacheilidae	complete mitochondrial genome
KX376479	*Triplophysa* sp.	Nemacheilidae	complete mitochondrial genome
KX354975	*Triplophysa stenura*	Nemacheilidae	complete mitochondrial genome
KT213604	*Triplophysa stenura*	Nemacheilidae	complete mitochondrial genome
KJ631324	*Triplophysa stewarti*	Nemacheilidae	complete mitochondrial genome
KT213605	*Triplophysa stewarti*	Nemacheilidae	complete mitochondrial genome
JQ663847	*Triplophysa stoliczkai*	Nemacheilidae	complete mitochondrial genome
KP979754	*Triplophysa strauchii*	Nemacheilidae	complete mitochondrial genome
KP297875	*Triplophysa strauchii*	Nemacheilidae	complete mitochondrial genome
KT224363	*Triplophysa tenuis*	Nemacheilidae	complete mitochondrial genome
KT122845	*Triplophysa tibetana*	Nemacheilidae	complete mitochondrial genome
KM212178	*Triplophysa tibetana*	Nemacheilidae	complete mitochondrial genome
KT224364	*Triplophysa tibetana*	Nemacheilidae	complete mitochondrial genome
KT259194	*Triplophysa ulacholica*	Nemacheilidae	complete mitochondrial genome
KT008666	*Triplophysa venusta*	Nemacheilidae	complete mitochondrial genome
PP203140	*Triplophysa weiheensis*	Nemacheilidae	complete mitochondrial genome
MW582823	*Claea wulongensis*	Nemacheilidae	Cyt *b*
OQ754129	*Claea wulongensis*	Nemacheilidae	Cyt *b*
KT224365	*Triplophysa wuweiensis*	Nemacheilidae	complete mitochondrial genome
KT751089	*Triplophysa xiangxiensis*	Nemacheilidae	complete mitochondrial genome
KT224366	*Triplophysa xichangensis*	Nemacheilidae	complete mitochondrial genome
OQ998934	*Triplophysa zhenfengensis*	Nemacheilidae	complete mitochondrial genome
MT992551	*Triplophysa zhenfengensis*	Nemacheilidae	complete mitochondrial genome
ON116501	*Troglonectes barbatus*	Nemacheilidae	complete mitochondrial genome
MG738689	*Troglonectes daqikongensis*	Nemacheilidae	complete mitochondrial genome
ON116505	*Troglonectes donglanensis*	Nemacheilidae	complete mitochondrial genome
ON116509	*Troglonectes duanensis*	Nemacheilidae	complete mitochondrial genome
ON116502	*Troglonectes elongatus*	Nemacheilidae	complete mitochondrial genome
ON116512	*Troglonectes furcocaudalis*	Nemacheilidae	complete mitochondrial genome
ON116523	*Troglonectes jiarongensis*	Nemacheilidae	complete mitochondrial genome
NC_058004	*Troglonectes longibarbatus*	Nemacheilidae	complete mitochondrial genome
ON116498	*Troglonectes macrolepis*	Nemacheilidae	complete mitochondrial genome
ON116494	*Troglonectes microphthalmus*	Nemacheilidae	complete mitochondrial genome
ON116511	*Troglonectes retrodorsalis*	Nemacheilidae	complete mitochondrial genome
ON116522	*Troglonectes shuilongensis*	Nemacheilidae	complete mitochondrial genome
ON116510	*Troglonectes translucens*	Nemacheilidae	complete mitochondrial genome

Table 2. Morphometric measurements for *Claea scet*, sp. nov, *C.dabryi*, *C.minibarba* and *C.wulongensis*.

Characteristics	*Claea scet* (n = 14)				*Claea dabryi* (n = 31)			*Claea minibarba* (n = 7) (Zhang et al. 2024)			*Claea wulongensis* (n = 8) (Guo et al. 2021)		
	Holotype	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.
Scales		Absent		/	Absent		/	Absent		/	Absent		/
Lateral line		Complete		/	Complete		/	Complete		/	Complete		/
Dorsal fin rays		III,8–9	III,8	/	III,7–8	III,7	/	III,8	III,8	/	III,8	III,8	/
Anal fin rays		III,5–6	III,5	/	II,5	II,5	/	II,5	II,5	/	I,5	I,5	/
Pectoral fin rays		I,10	I,10	/	I,8–9	I,8	/	I,10	I,10	/	I,8–9	I,8–9	/
Pelvic fin rays		I,5–6	I,6	/	I,5–6	I,6	/	I,6	I,6	/	I,5–7	I,5–7	/
Caudal fin rays		2+16	2+16	/	2+15–17	2+16	/	2+16	2+16	/	2+16	2+16	/
Standard length (SL,mm)	51.3	34.2–58.9	50.9	4.7	37.6–88.5	60.5	14.4	48.8–69.9	62.6	6.6	49.0–67.2	55.7	6.2
In percentage of SL (%)													
Head Length	24.6	20.8–25.5	23.4	1.4	20.4–24.8	23.8	1.0	21.1–23.3	21.9	1.0	20.4–23.5	22.6	1.0
Body depth	13.5	10.1–13.6	11.7	1.1	9.6–15.0	12.5	1.4	14.7–17.6	15.9	1.0	9.3–13.6	12.1	1.3
Predorsal length	54.6	50.0–56.3	54.0	2.0	49.0–59.1	52.9	2.0	50.5–54.0	52.4	1.3	50.4–54.2	51.9	0.9
Prepelvic length	51.7	50.2–56.0	53.6	1.6	47.1–53.1	49.8	1.6	47.7–50.6	49.8	1.6	48.3–50.9	49.7	0.9
Preanal length	77.0	73.4–77.9	75.9	1.1	71.6–78.4	74.5	1.7	72.7–75.2	73.9	1.0	71.5–77.7	73.4	1.8
Dorsal-fin height	11.8	9.4–19.3	13.6	3.9	16.1–22.2	18.8	1.3	15.8–18.1	16.8	0.8	15.0–19.8	16.2	1.5
Dorsal-fin base length	12.0	8.4–12.5	11.1	1.0	9.4–13.3	11.3	1.0	10.8–12.3	11.6	0.6	10.7–13.4	12.4	0.9
Anal-fin height	8.0	7.0–8.4	7.7	0.4	13.8–20.0	16.4	1.4	13.6–15.7	14.8	0.7	12.4–16.5	14.5	1.3
Anal-fin base length	9.1	8.4–9.6	8.3	0.8	5.6–10.6	8.0	1.0	7.8–9.0	8.1	0.4	6.6–8.2	7.4	0.6
Pelvic-fin length	14.9	12.2–15.5	13.8	1.0	13.3–17.6	14.9	0.9	12.5–15.1	13.8	0.8	12.5–14.5	13.2	0.6
Pectoral-fin length	20.1	16.7–22.0	19.1	1.2	18.3–22.3	17.6	1.4	15.0–17.6	16.8	0.9	15.6–18.4	17.6	1.0
Caudal-fin length	17.8	15.7–20.5	17.9	1.7	17.4–23.4	20.0	1.4	15.2–18.1	17.2	1.0	15.9–20.8	18.1	1.3
Caudal-peduncle length (CPL)	16.1	14.4–18.9	15.9	1.2	15.4–22.3	17.9	1.4	18.0–20.5	19.2	1.0	14.2–20.7	16.6	1.2
Caudal-peduncle depth (CPD)	8.2	5.5–8.5	7.0	0.9	5.5–10.3	8.3	1.0	9.5–11.7	10.7	0.7	7.6–9.4	8.5	0.7
In percentage of HL (%)													
Head depth	44.4	40.4–56.1	45.6	4.4	39.6–52.0	44.9	3.0	55.5–59.4	57.5	1.6	45.3–54.2	50.6	2.9
Head width	60.3	51.6–77.0	59.8	7.2	45.9–59.7	53.4	3.6	61.5–68.0	64.0	2.1	55.7–65.8	62.4	3.5
Snout length	40.2	28.6–44.7	37.8	5.4	35.7–45.2	41.0	2.5	42.3–46.3	45.0	1.3	38.9–45.0	41.9	1.9
Eye diameter	5.6	3.8–5.9	5.1	0.9	13.7–23.3	17.8	2.6	15.8–18.4	16.9	0.9	11.1–19.1	17.0	2.1
Interorbital width	27.1	18.3–31.9	25.6	4.3	22.8–26.3	27.3	2.5	30.3–36.3	32.6	2.2	38.5–43.1	41.3	1.5
Maxillary barbel length	25.4	22.4–34.9	26.0	3.5	29.8–47.4	34.9	3.9	21.5–29.6	26.9	2.7	21.8–35.9	29.8	3.2
Inner rostral barbel length	17.1	11.5–20.4	16.3	2.5	15.6–24.7	20.2	2.4	16.0–21.7	18.8	2.5	16.5–23.4	21.6	1.2
Outer rostral barbel length	26.8	23.0–32.8	27.5	3.5	30.2–47.5	37.9	3.9	22.1–28.0	25.1	2.4	21.4–41.5	32.4	4.5
CPD/CPL (%)	51.2	34.4–52.8	44.2	5.7	33.7–53.4	46.5	4.3	50.8–61.2	55.6	3.7	44.3–57.4	51.2	4.5

Results

Taxonomic account

Family Nemacheilidae Regen, 1911
Genus *Claea* Sauvage, 1874

***Claea scet* sp. nov.**

https://zoobank.org/AADDEC5A-A9BC-4F7D-976F-4FE0CDD79299

Holotype. • IHB 202305300005, 51.3 mm SL; a subterranean tributary of the Dadu River in the Yangtze River drainage in Taojin Cave, Shiqianggou, Hulu Town, Shawan District, Leshan City, Sichuan Province, China (29°17'47.0"N 103°38'13.0"E; 570 m elevation); collected by Li He & Ze-Yu Li, 28.V.2023.

Paratypes. • IHB 202305300001–202305300004, IHB 202305300006–202305300009, 8, 43.1–56.4 mm SL; other data same as holotype; • IHB 202305300010–202305300016, 7, 34.2–58.9 mm SL; same locality as holotype, collected by Yuan Li & Ze-Yu Li, VI-16-2024.

Diagnosis. *C. scet* resembles all known species of *Claea* in possessing a processus dentiformis at the medium of the upper jaw, absence of tubercle-bearing, elevated skin on the sides of the head and a thickened tuberculated pad on the dorsal surface of the thickened and widened rays of the pectoral fin in males, absence of adipose crest between dorsal fin and caudal fin base, body scaleless, and absence of supra-pelvic flap, all of which are diagnostic features of *Claea*. *C. scet* can be distinguished from *C. dabryi*, *C. minibarba* and *C. wulongensis* by the combination of the following characters (see Table 2): Processus dentiformis reduced, not covering lower jaw when mouth shut; eye vestigial, diameter of eye 3.8–5.9% SL; short anal fin, anal fin height 7.0–8.4% SL. *C. scet* is further distinguished from *C. dabryi* by shorter maxillary barbels (22.4–27.5% SL *vs.* 29.8–47.4% SL) and shorter outer rostral barbels (23.0–29.8% SL *vs.* 30.2–47.5% SL). *C. scet* is further distinguished from *C. minibarba* by a more depressed body (body depth 10.1–13.5% SL *vs.* 14.7–17.6% SL), a more posteriorly situated pelvic fin (prepelvic length 51.7–56.0% SL *vs.* 47.7–50.6% SL), a longer pectoral fin (17.6–20.2% SL *vs.* 15.0–17.6% SL), a shallower

caudal peduncle (5.5–8.5% SL *vs.* 9.5–11.7% SL) and a more elongated head (head depth 41.4–46.5% HL *vs.* 55.5–59.4% HL and head width 52.3–60.3% HL *vs.* 61.5–68.0% HL). *C. scet* is further distinguished from *C. wulongensis* by a more posteriorly situated pelvic fin (prepelvic length 51.7–56.0% SL *vs.* 48.3–50.9% SL), a longer anal fin base (8.4–9.6% SL *vs.* 6.6–8.2% SL), more closely situated eyes (interorbital length 23.5–31.9%HL *vs.* 38.5–43.1% HL).

Description. Morphometric data for 16 type specimens of *C. scet* are provided in Suppl. material 1. Juvenile individuals with a standard length (SL) of less than 40 mm were excluded from morphological comparisons with congeners (Table 2). The general body profile is illustrated in Fig. 1. The body is elongated, subcylindrical anteriorly, and laterally compressed posteriorly. The dorsal profile of the head is nearly straight, while the dorsal profile of the body is convex. The ventral profile is almost straight from the snout tip to the anal fin origin, with a slight concavity posterior to the anal fin origin. The greatest body depth occurs anterior to the dorsal fin origin, gradually decreasing toward the caudal fin base. The body is entirely scaleless and smooth, with a complete and straight lateral line. The cephalic lateral line system comprises 3 + 8 infraorbital, 6 supraorbital, 3 supratemporal, and 10 preopercular-mandibular pores (Fig. 2).

The head is moderately depressed, longer than wide, and wider than deep. The snout is pointed, with a snout length measuring 38.1–44.7% of the head length (HL). The eyes are reduced, with a diameter of 3.8–5.9% HL, and are positioned dorsolaterally on the head. Both anterior and posterior nostrils are closely situated; the anterior nostril is housed in a short tube with an elongated, tube-like tip that does not reach the anterior margin of the eye. The mouth is inferior and curved, with thin lips exhibiting shallow surface furrows. The upper lip is complete and connected to the lower lip at the corners of the mouth. The lower lip features a distinct V-shaped median incision. The upper and lower jaws are arched, with a weakly developed processus dentiformis on the upper jaw compared to congeners (Figs 2, 3), not covering the lower jaw when mouth is shut. Three pairs of barbels are present: two pairs of rostral barbels (the inner pair not reaching the corner of the mouth, and the outer pair slightly longer than the inner pair) and one pair of maxillary barbels, which extend to the posterior margin of the eye when fully extended (Fig. 2).

Figure 1. Morphological characters of holotype, IHB 202305300005 of *Claea scet* sp. nov. in preservative (10% formalin). **A.** Lateral view; **B.** Dorsal view; **C.** Ventral view

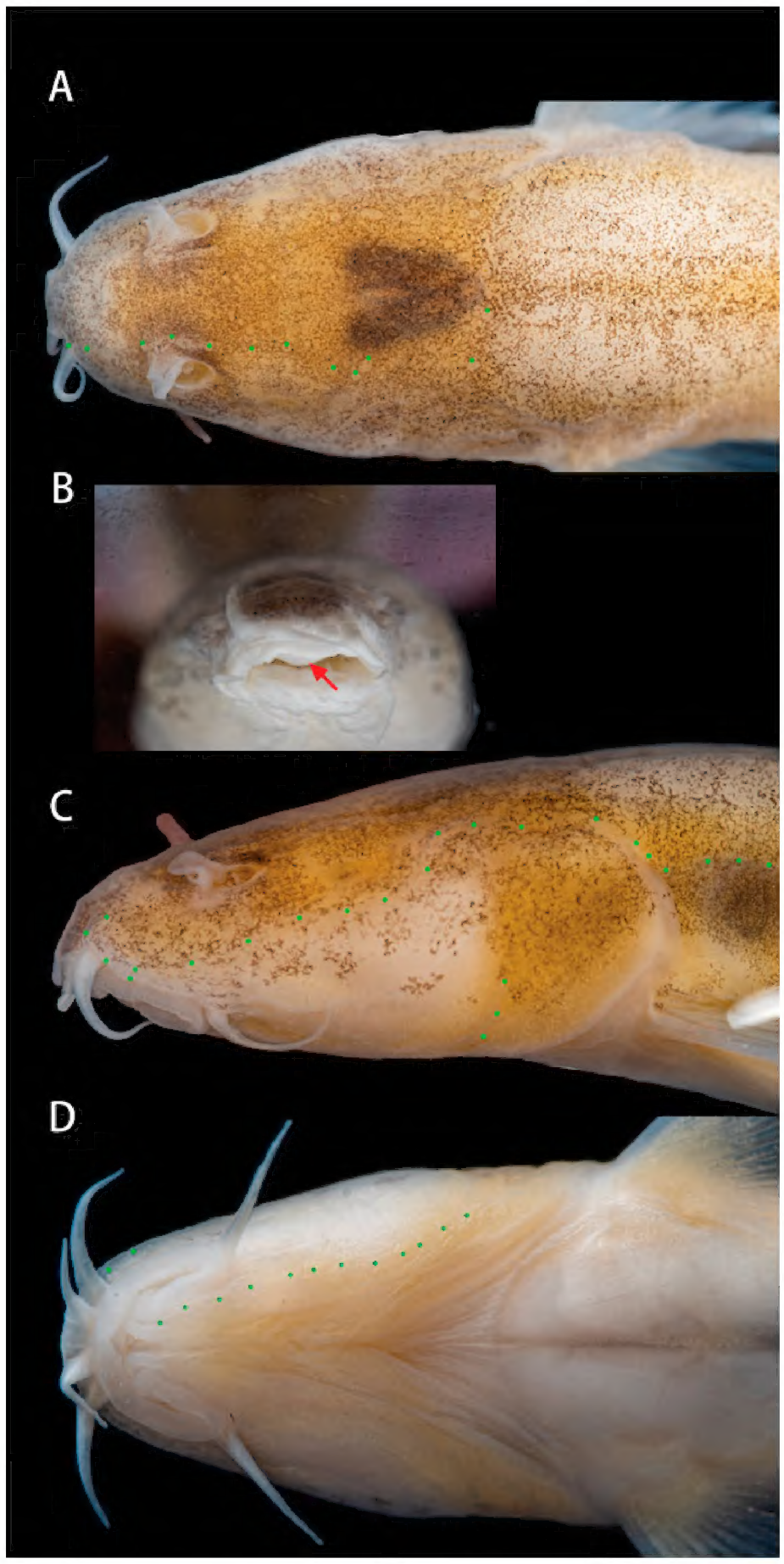

Figure 2. Detailed cephalic morphology of holotype, IHB 202305300005 of *Claea scet* sp. nov. **A.** Dorsal side view of head; **B.** Frontal view of head, processus dentiformis shown by a red arrow; **C.** Lateral sideview of head, and **D.** Ventral side view of head (Cephalic lateral line system highlighted as green dots).

Dorsal fin with 3 simple and 8 (n = 12) or 9 (n = 4) branched fin rays, origin behind mid-point between snout tip and caudal-fin base and posterior to the pelvic fin origin, distal margin truncate, length of dorsal fin greater than body depth. Pelvic fins with 1 simple and 5 (n = 1) or 6 (n = 15) branched fin rays, origin closer to anal fin origin than pectoral fin origin, tips of pelvic fins not reaching anus. Pectoral fins with 1 simple and 10 branched fin rays, extending beyond the halfway to pelvic-fin origin. Anal fin with 3 simple and 5 (n = 7) or 6 (n = 8) branched fin rays, origin closer to pelvic-fin insertion than to caudal fin base. Caudal fin forked, with 2 simple and 16 branched fin rays, the upper lobe slightly longer than the lower (Figs 1, 6).

Intestine short, without bend or loops immediately posterior to stomach. Bony capsule of the air bladder large and thin, dumbbell-shaped, (Fig. 5), posterior chamber of air bladder degenerated. Vertebrae 4 + 38 (Fig. 4).

Coloration. In their natural subterranean aquatic habitats, live specimens exhibit a general body coloration of light gray with a faint pinkish hue, accompanied by sparse pigmentation distributed laterally and dorsally. The ventral region is semi-transparent, while all fins appear hyaline. In specimens preserved in 10% formalin, the body coloration transitions to light gray with a moderate yellowish tint, and pigmentation is observed to fade in some individuals (Figs 1, 6).

Distribution. This species is presently only known from a subterranean tributary of the Dadu River in the upper Yangtze River in Taojin Cave, Shiqianggou, Hulu Town, Shawan District, Leshan City, Sichuan Province, China (Figs 7, 9).

Etymology. The specific name "scet" is in reference to the abbreviation of Sichuan Cave Exploration Team, a cave exploration team who collected the type specimens, in recognition of their contributions to the understanding of cave fishes of Sichuan Province. "川洞山鰍 (Pinyin: Chuan Dong Shan Qiu)" is proposed for the Chinese common name of this new species.

Field notes. The Taojin Dolomite Cave, situated adjacent to a backroad in Shiqianggou, is characterized as a shaft-type cave with a broad entrance. Access to the cave is restricted to the Single Rope Technique (SRT) for descent. During the rainy season, elevated water levels render the cave inaccessible, while at other times, the interior remains

Figure 3. Comparison of processus dentiformis of different *Claea*. spp. **A.** *C. scet*, 51.28 mm SL, IHB 202305300005; **B.** *C. dabryi* 98.35 mm SL, IHB 81VII2537; **C.** *C. minibarba*, 62.31 mm SL, IHB 202204288315.

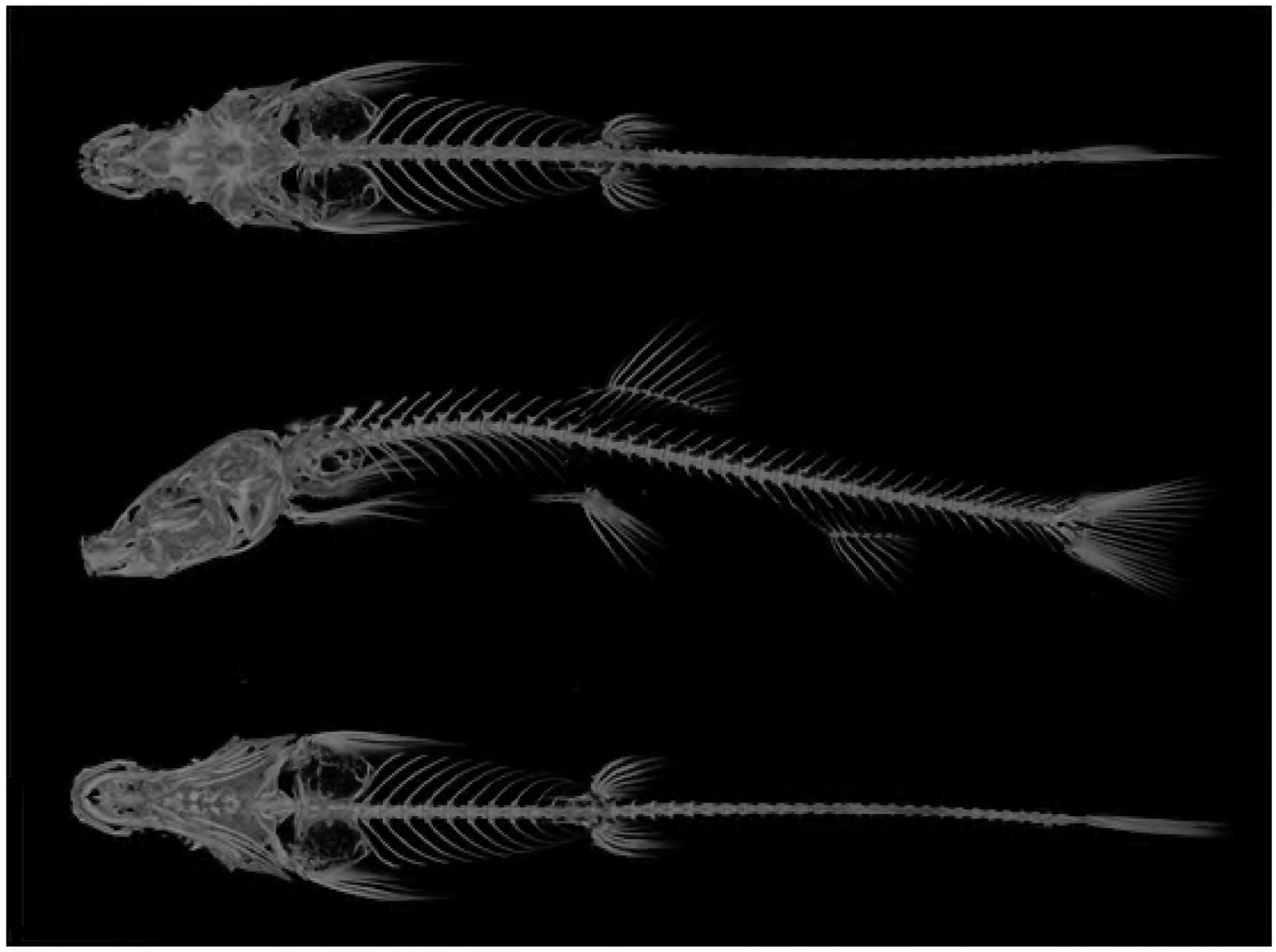

Figure 4. Dorsal, lateral and ventral views of the micro-CT graph of the skeleton of holotype IHB 202305300005 of *Claea scet* sp. nov.

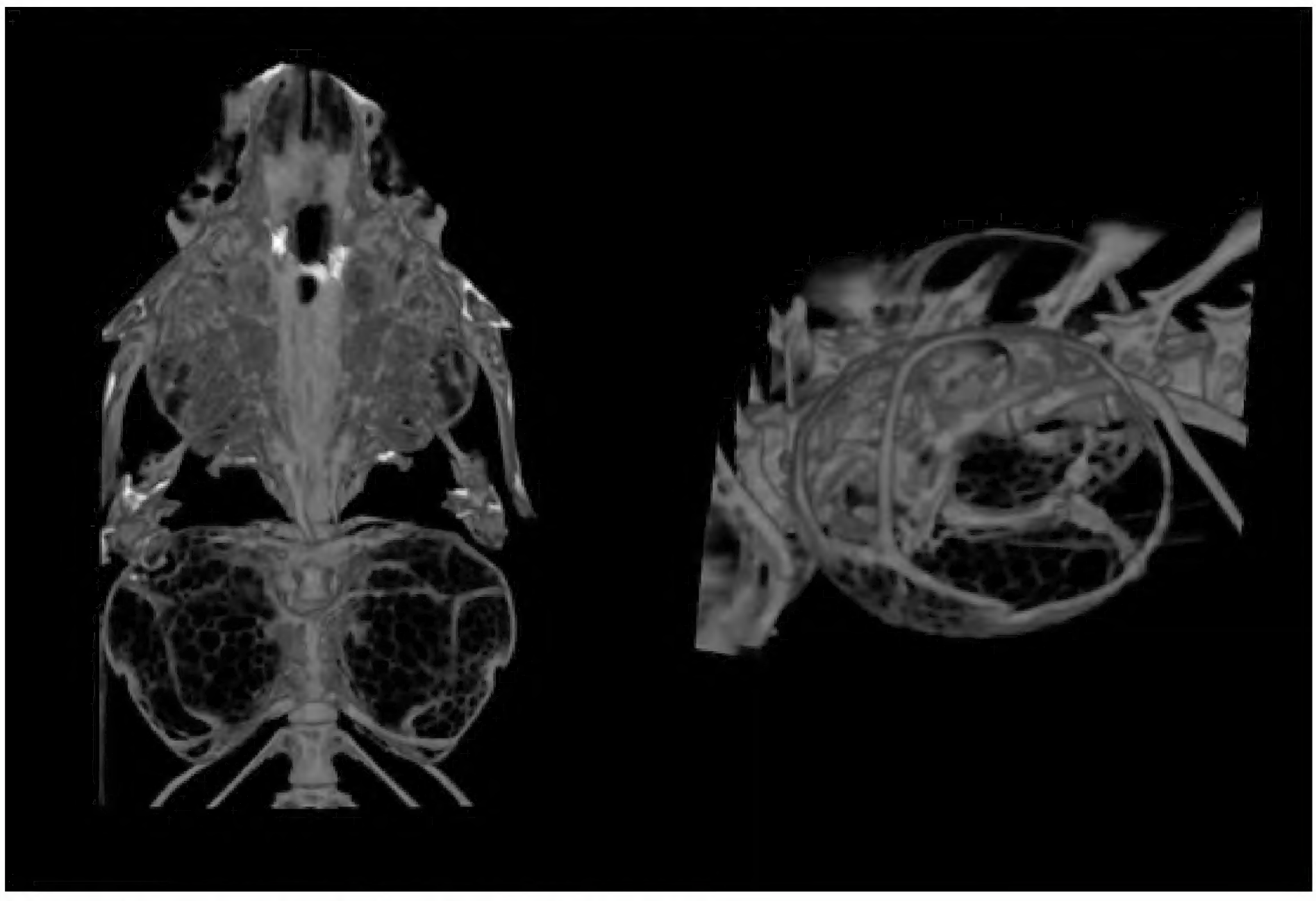

Figure 5. Dorsal and lateral profile of Bony capsule of the air bladder.

Figure 6. *Claea scet* sp.nov. in life, paratype IHB 202305300009. Photo from Jiajun Zhou.

humid with spacious tunnels. This species inhabits pools located within the deep dark zone of the cave, where environmental conditions during the survey period in May 2023 included an air temperature of 18–19 °C and a water temperature of 15 °C (Fig. 7). Other troglobites found inside the same cave were *Jujiroa duqianae* Tian & He, 2023 (Coleoptera, Carabidae), *Paratachys* sp. (Coleoptera, Carabidae), *Domene lizeyui* Wang & He, 2024 (Coleoptera, Staphylinidae), *Epanerchodus* sp. (Polydesmida, Polydesmidae), and *Chetoneura* sp. (Diptera, Keroplatidae).

Molecular phylogeny

Both phylogenetic methods (ML and BI) recovered a similar tree topology (Fig. 8) based on two mitochondrial gene fragments (Cyt *b*, *COI*). All *Claea* species formed a monophyly (except for GenBank accession no. KT906089 of *C. dabryi*, collected from Gaoyanzi River in Pengzhou, Chengdu City, Sichuan Province, China (31°2'59.89"N, 104°0'58.55"E, which could be misidentified.) with strong support, and as the sister group to the hypogean *Triplophysa* species. Although the genus *Triplophysa* is non-monophyletic, all hypogean *Triplophysa* and non-cavefishes separate into monophyletic clades. The monophyly of the new species is strongly supported. Phylogenetic analyses supported the new species, *C. scet* being a closely related sister species of *C. dabryi* from the Jinsha River (the upper Yangtze River). The average genetic distance (*p*-distance) between the new species and other *Claea* species ranges from 1.95% (with *C. dabryi*) to 6.02% (*C. wulongensis*) for Cyt *b* (Table 3).

Key to the species of *Claea*

A key to four species of *Claea* is shown below.

1 Processus dentiformis reduced, not covering lower jaw when mouth shut ..... *C. scet*
– Processus dentiformis prominent, covering lower jaw when mouth shut 2
2 Interorbital length larger than 38% HL ..... *C. wulongensis*
– Interorbital length lesser than 38% HL 3
3 Maxillary barbels extending to the middle of eye ..... *C. minibarba*
– Maxillary barbels extending beyond posterior margin of eye ..... *C. dabryi*

Discussion

Discovery of the first troglobitic fish species from the karst regions north of the Yangtze River, China.

The limestone caves and subterranean water systems of southwestern China's extensive karst regions harbor more than 170 endemic cavefish species across two orders (Cypriniformes, Siluriformes) and five families (Balitoridae, Cyprinidae, Nemacheilidae, Cobitidae, Amblycipitidae) (Ma et al. 2019; Luo et al. 2023b). Notably, all documented Chinese cavefish species are confined to karstic zones south of the Yangtze River, particularly within the upper Pearl, upper Red, and upper Yangtze River basins. Of the 14 troglobitic fish species recorded from the Yangtze River system (Table 4), all originate from the mainstream or southern-bank tributaries, including *Sinocyclocheilus sanxiaensis* (Three Gorges Reservoir), *Claea wulongensis* (Wujiang River), and *Triplophysa xiangxiensis* (Yuanjiang River) (Yang et al. 1986; Jiang et al. 2019; Chen et al. 2021). The discovery

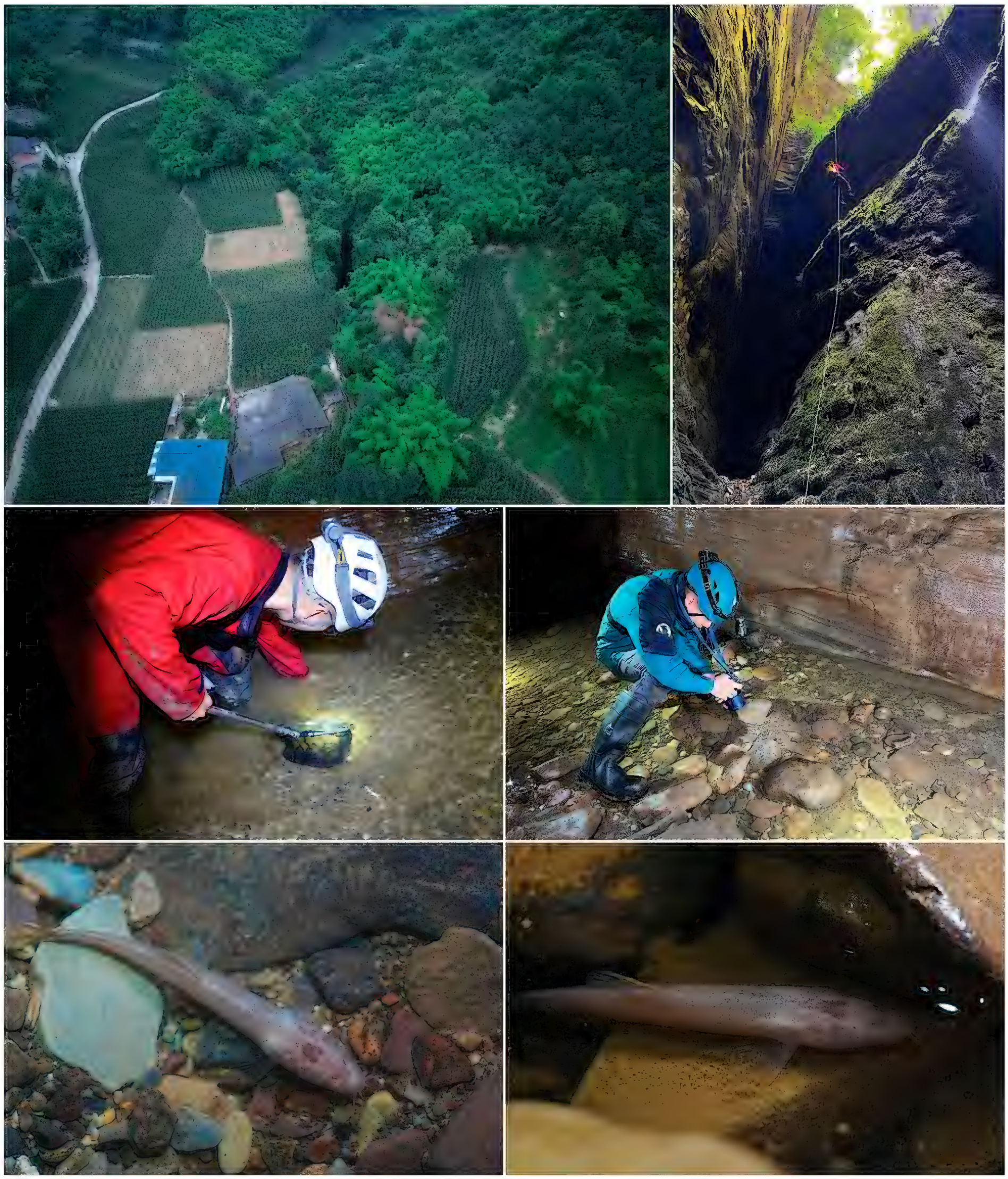

Figure 7. Taojin Cave, the type locality of *Claea scet* sp.nov. and individuals of *Claea scet* sp.nov. found in the cave. **A.** environs of the cave; **B.** Li He descending into the cave using SRT; **C.** Author collecting *Claea scet* sp.nov. with hand-net; **D.** Author filming live image of *Claea scet* sp. nov.; **E, F.** Individuals of *Claea scet* sp.nov. resting on gravelly bottom of the subterranean river in Taojin.

of *Claea scet*—the first cavefish recorded from northern tributaries of the Yangtze River—significantly expands the known biogeographic range of Chinese cavefishes (Fig. 9). Given the extensive limestone cave networks within the Sichuan Basin, Wushan Mountains, and Daba Mountains, systematic ichthyofaunal surveys in these regions are expected to yield critical insights into the diversity and evolution of Yangtze River cavefish assemblages.

Table 3. The average pairwise *p*-distances (the number of substitutions per site with pairwise) between species of *Claea* based on Cyt b gene sequences.

	C. minibarba	***C. dabryi***	***C. scet***	***C. wulongensis***
C. minibarba	/			
C. dabryi	0.0600	/		
C. scet	0.0591	0.0195	/	
C. wulongensis	0.0439	0.0584	0.0602	/

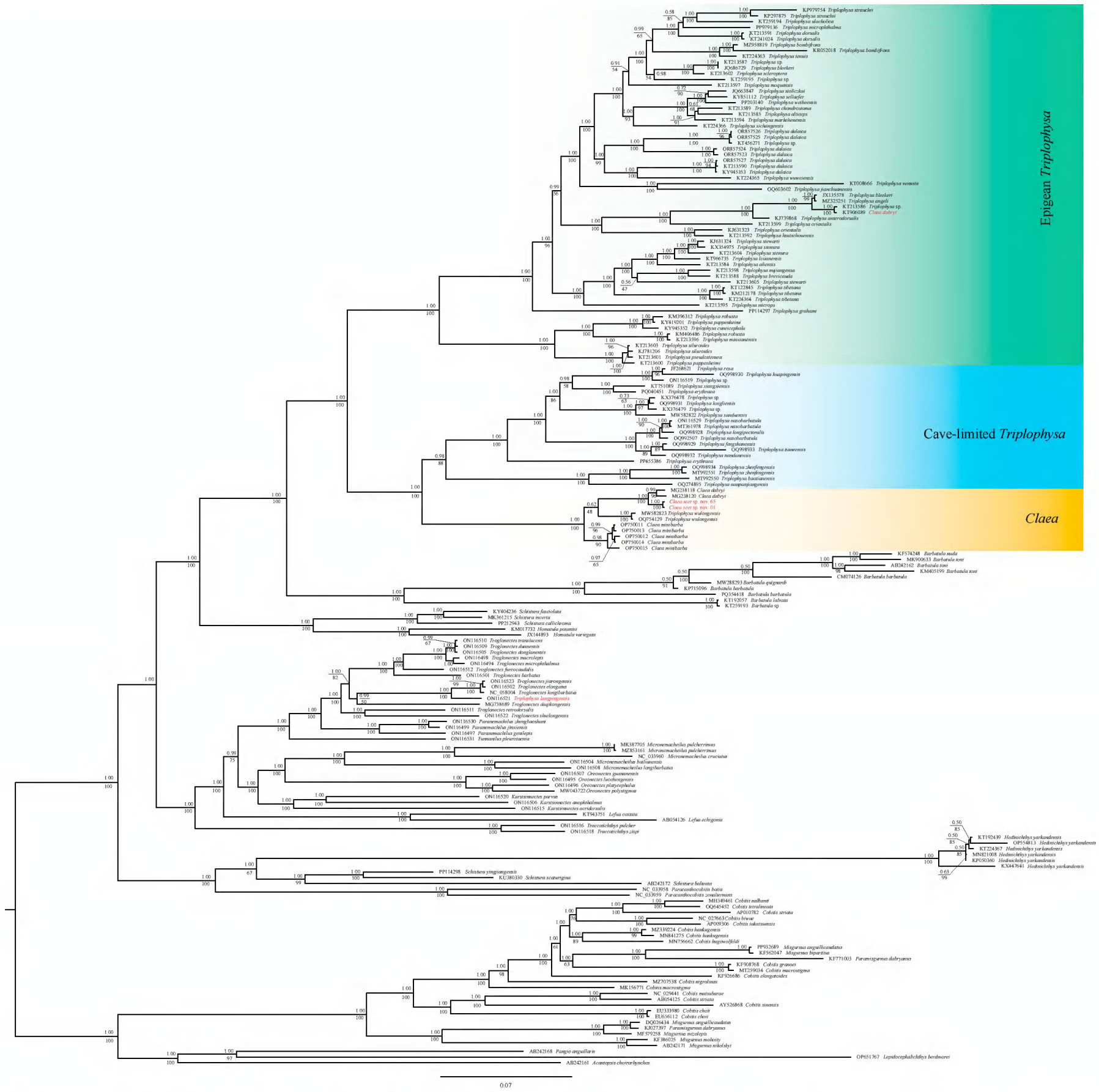

Figure 8. Phylogenetic tree of *Claea*, both epigean and hypogean *Triplophysa* and other closely related congeners reconstructed based on combined two mitochondrial (Cyt *b* and *CO*I) gene fragments. Ultrafast bootstrap (UFB) supports from maximum likelihood (ML) analyses/Bayesian posterior probabilities (BPP) from Bayesian inference (BI) analyses are noted beside nodes. The scale bar represents 0.07 nucleotide substitutions per site.

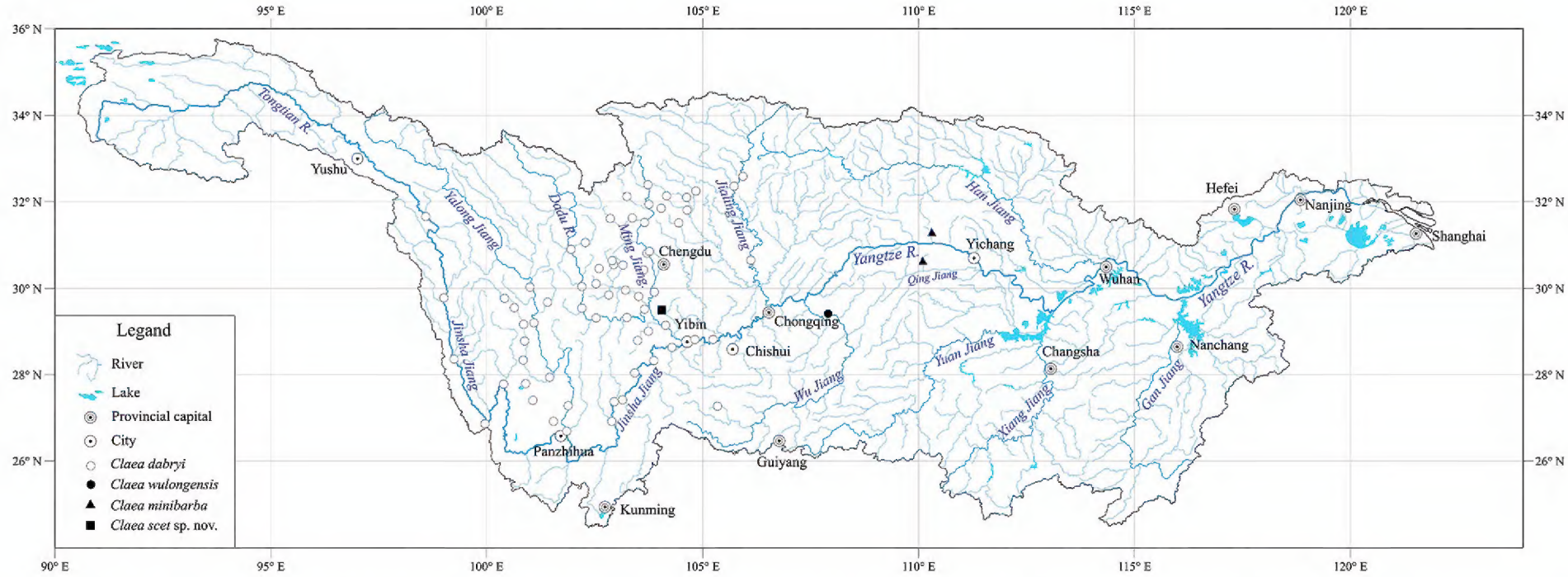

Figure 9. Distribution and hydrology of the type locality of *Claea scet* sp. nov. (square), *C. wulongensis* (black circle), *C. minibarba* (triangle) and known distribution of *C. dabryi* (white circle).

Table 4. List of locality information of known cavefish species from the Yangtze River basin.

Species	Familly	Type locality	Tributary	Reference
Claea scet	Nemacheilidae	Shawan District, Leshan City, Sichuan Province, China	Dadu River	This study
Claea wulongensis	Nemacheilidae	Wulong County, Chongqing City,China	Wujiang River	Chen et al. 2021
Sinocyclocheilus grahami	Cyprinidae	Dianchi Lake, Kunming City, Yunnan Province, China	Jinshajiang River	Zhao & Zhang, 2009
Sinocyclocheilus guiyang	Cyprinidae	Qingzhen County, Guiyang City, Guizhou Province, China	Wujiang River	Shao et al. 2024
Sinocyclocheilus huizeensis	Cyprinidae	Huize County, Qujing City, Yunnan Province, China	Niulanjiang River	Cheng et al. 2015
Sinocyclocheilus multipunctatus	Cyprinidae	Guizhou Province, China	Wujiang River	Zhao & Zhang, 2009
Sinocyclocheilus sanxiaensis	Cyprinidae	Zigui County, Hubei Province, China.	Mainstream of Yangtze River	Jiang et al. 2019
Sinocyclocheilus wumengshanensis	Cyprinidae	Xundian Hui and Yi Autonomous County, Kunming City, Yunnan Province, China	Niulanjiang River	Li et al. 2003
Triplophysa erythraea	Nemacheilidae	Huaren County, Xiangxi Tujia and Miao Autonomous Prefecture, Hunan province, China	Yuanjiang River	Huang et al. 2019
Triplophysa qingzhenensis	Nemacheilidae	Qingzhen County, Guiyang City, Guizhou Province, China	Wujiang River	Liu et al. 2022
Triplophysa qini	Nemacheilidae	Fengdu County, Chongqing City, China	Wujiang River	Deng et al. 2022
Triplophysa rosa	Nemacheilidae	Wulong County, Chongqing City, China	Wujiang River	Chen et al. 2005
Triplophysa xiangxiensis	Nemacheilidae	Longshan County, Xiangxi Tujia and Miao Autonomous Prefecture, Hunan province, China	Yuanjiang River	Yang et al. 1986
Triplophysa wudangensis	Nemacheilidae	Wudang Distinct, Guiyang City, Guizhou Province, China	Wujiang River	Liu et al. 2022

Historically, cavefish research in China has centered on Guangxi and Yunnan provinces, while studies of Sichuan's subterranean fauna have primarily focused on invertebrates (Hou et al. 2006; Deuve et al. 2020; Yang et al. 2023; Wang and He 2024). Prior to this study, no obligatory troglobitic fish had been documented in Sichuan. The discovery of *C. scet* as the province's first cavefish species underscores the potential for undiscovered troglobitic fish diversity within Sichuan's subterranean hydrological networks, warranting intensified exploration of these understudied ecosystems.

Discovery of the first obligatory troglobitic member of *Claea* provides potential novel perspective of evolution of nemacheilid cavefishes

The genus *Claea* comprises predominantly epigean species, with only two exceptions documented in subterranean environments: *C. wulongensis* and the newly described *C. scet*. Notably, *C. wulongensis* lacks definitive troglomorphic adaptations, rendering *C. scet* the sole obligatory troglobitic member of the genus. Phylogenetic reconstructions reveal a sister-group relationship between *Claea* and hypogean *Triplophysa* lineages, with both genera forming distinct monophyletic clusters that further group with epigean *Triplophysa* species. This topology aligns with prior molecular analyses (Xiong et al. 2017; Yan 2017; Chen et al. 2019; Guo 2021; Zhang et al. 2024). Contrasting with the monophyletic assemblage of hypogean *Triplophysa*, the two hypogean *Claea* species (*C. scet* and *C. wulongensis*) do not form a sister group (Fig. 7). Instead, *C. scet* demonstrates closer genetic affinity to the epigean *C. dabryi* from the Jinsha River drainage, suggesting independent evolutionary origins of troglomorphic traits within *Claea*. The minimal pairwise genetic divergence (*p*-distance = 1.95%) between *C. scet* and *C. dabryi* supports a recent speciation event (Fig. 8, Table 3).

While *Triplophysa*—the nemacheilid genus with the highest diversity of hypogean species—has been extensively studied for cave adaptation patterns (Shi et al. 2018; Zhang et al. 2024), persistent questions regarding its monophyly (as evidenced by phylogenetic analyses) highlight the significance of discovering a troglobitic *Claea* species as a novel model system for investigating subterranean adaptation mechanisms in Nemacheilidae.

Beyond canonical troglomorphic traits (e.g., reduced pigmentation and eyes), *C. scet* exhibits unique morphological features absent in congeners, including a reduced processus dentiformis (Fig. 3). Its fins and barbels, however, do not enlarge to serve as sensory organs as they are on many other cavefishes, with sizes that do not exhibit a prominent difference compared with epigean congeners. The functional significance of these morphological innovations warrants comprehensive investigation through integrated studies of physiology, ecological interactions, and behavioral ecology in this newly described taxon.

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References

Aljanabi SM, Martinez I (1997) Universal and rapid salt-extraction of high-quality genomic DNA for PCR-based techniques. Nucleic Acids Research 25(22): 4692–4693. https://doi.org/10.1093/nar/25.22.4692

Bănărescu P, Nalbant TT (1976) The genus *Oreias* Sauvage, 1874 (Pisces, Cobitidae). Nymphaea 4: 185–193. [pls. 1–2]

Cao WX, Wu XW (1962) An investigation of the fish biology and fishery problems in Ganze-Apa region of western Szechuan Province [J]. Acta Zootaxonomica Sinica 2: 79–112. https://doi.org/10.3724/issn1000-3207-1962-2-79-4

Chen YY (1998) The fishes of the Hengduan Mountains Region. Science Press, Beijing. [In Chinese, English abstract]

Chen XY, Yang JX (2005) *Triplophysa rosa* sp. nov.: a new blind loach from China. Journal of Fish Biology 66: 599–608. https://doi.org/10.1111/j.0022-1112.2005.00622.x

Chen L, Lu ZM, Mao WN (2006) A new species of *Schistura* discovered in Yunnan, China. Guizhou Agricultural Sciences 34(5): 54–55. [In Chinese, English abstract]

Chen W, Yang J, Li Y, Li X (2019) Exploring taxonomic diversity and biogeography of the family Nemacheilinae (Cypriniformes). Ecology and Evolution 9(18): 10343–10353. https://doi.org/10.1002/ece3.5553

Chen S, Sheraliev B, Shu L, Peng Z (2021) *Triplophysa wulongensis*, a new species of cave-dwelling loach (Teleostei, Nemacheilidae) from Chongqing, Southwest China. ZooKeys 1026: 179–192. https://doi.org/10.3897/zookeys.1026.61570

Cheng C, Pan XF, Chen XY, Li JY, Ma L, Yang JX (2015) A new species of the genus *Sinocyclocheilus* (Teleostei:Cypriniformes), from Jinshajiang Drainage, Yunnan, China. Cave Research 2(4): 1–4.

Chu, XL Chen YR (1990) The fishes of Yunnan, China. Part II. Science Press, Beijing, 313 pp. [In Chinese]

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9(8): 772. https://doi.org/10.1038/nmeth.2109

Deng SQ, Wang XB, Zhang E (2022) *Triplophysa qini*, a new stygobitic species of loach (Teleostei: Nemacheilidae) from the upper Chang-Jiang Basin in Chongqing, Southwest China. Ichthyological Exploration of Freshwaters, IEF–1178, 1–11.

Deuve T, He L, Tian MY (2020) Descriptions of the first semi-aphenopsian troglobiotic Patrobini and of a new anophthalmic cave-dwelling Trechini from central Sichuan, China (Coleoptera: Caraboidea), Annales de la Société entomologique de France (N.S.) 56(2): 93–105. https://doi.org/10.1080/00379271.2020.1722748

Ding RH, Deng QX (1990) The Noemacheilinae Fishes From Sichuan,With Description of A New Species I. *Paracobitis*, *Nemacheilus* and *Oreias* (Cypriniformes: Cobitidae). Zoological Research 11(4): 285–287.

Du LN, Yang J, Min R, Chen XY, Yang JX (2021) A review of the Cypriniform tribe Yunnanilini Prokofiev, 2010 from China, with an emphasis on five genera based on morphologies and complete mitochondrial genomes of some species. Zoological Research 42(3): 310–334. https://doi.org/10.24272/j.issn.2095-8137.2020.229

Du LN, Li SJ, Xu F, Luo T, Yu GH, Zhou J (2023) Clarification of Phylogenetic Relationships among Chinese Nemacheilids with Tube-Shaped Anterior Nostrils, with a Description of a New Genus and Two New Species. Journal of Zoological Systematics and Evolutionary Research 2023(2): 1–11. https://doi.org/10.1155/2023/3600085

Guo YS (2021) Colored Atlas of Fishes in Sichuan, Vol II. 505–507. Science Press, Beijing. [In Chinese]

He DK, Chen YF (2009) Phylogeography of *Schizothorax o'connori* (Cyprinidae: Schizothoracinae) in the Yarlung Tsangpo River, Tibet. Hydrobiologia 635(1): 251–262. https://doi.org/10.1007/s10750-009-9918-2

Hoa NT, Hao NV, Thuong HT (2012) Two new species of *Oreias* Sauvage, 1874 discovered in Son La city, Vietnam. Academia Journal of Biology32(4): 45–53. https://doi.org/10.15625/0866-7160/v32n4.720

Hou Z, Platvoet D, Li S (2006) *Gammarus abstrusus* n. sp., a new cave-dwelling gammaridean amphipod from Sichuan, China (Amphipoda, Gammaridea). Crustaceana 79(10): 1209–1222. https://doi.org/10.1163/156854006778859605

Huang TF, Zhang PL, Huang XL, Wu T, Gong XY, Zhang YX, Peng QZ, Liu ZX (2019) A new cave-dwelling blind loach, *Triplophysa erythraea* sp. nov. (Cypriniformes: Nemacheilidae), from Hunan Province, China. Zoological Research 40(4): 331–336. https://doi.org/10.24272/j.issn.2095-8137.2019.049

Jiang WS, Li J, Lei XZ, Wen ZR, Han YZ, Yang JX, Chang JB (2019) S*inocyclocheilus sanxiaensis*, a new blind fish from the Three Gorges of Yangtze River provides insights into speciation of Chinese cavefish. Zoological Research 40(6): 552–557. https://doi.org/10.24272/j.issn.2095-8137.2019.065

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. https://doi.org/10.1093/molbev/mst010

Kottelat M (2011) *Claea*, a new replacement name for *Oreias* Sauvage, 1874 (Teleostei: Nemacheilidae). Ichthyological Exploration of Freshwaters 21(4): 384.

Kottelat M (2012) Conspectus cobitidum: an inventory of the loaches of the world (Teleostei: Cypriniformes: Cobitoidei). The Raffles Bulletin of Zoology 26: 1–199.

Lan JH, Gan X, Wu TJ, Yang J (2013) Cave Fishes of Guangxi, China. Science Press, Beijing, 266 pp. [In Chinese]

Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG (2007) Clustal W and Clustal X version 2.0. Bioinformatics (Oxford, England) 23(21): 2947–2948. https://doi.org/10.1093/bioinformatics/btm404

Larsson A (2014) AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics (Oxford, England) 30(22): 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

Li WX, Mao WN, Lu ZM, Yan WZ (2003) The two new species of *Sinocyclocheilus* from Yunnan, China. Journal of Jishou University 24(2): 63–65. [Natural Science Edition] [In Chinese, English abstract]

Liao JW, Wang DZ, Luo ZF (1997) A new species and a new subspecies of *Schistura* [sic] from Guangxi and Guizhou, China (Cypriniformes: Cobitidae: Nemacheilinae). Acta Academiae Medicinae Zunyi 20(2–3): 4–7. [In Chinese, English summary]

Liu SW, Pan XF, Yang JX, Chen XY (2017) A new cave-dwelling loach, *Triplophysa xichouensis* sp. nov. (Teleostei Nemacheilidae) from Yunnan, China. Journal of Fish Biology 90(3): 834–846. https://doi.org/10.1111/jfb.13201

Liu F, Zeng Z, Gong Z (2022) Two new hypogean species of *Triplophysa* (Cypriniformes: Nemacheilidae) from the River Yangtze drainage in Guizhou, China. Journal of Vertebrate Biology 71: 22062.1–14. https://doi.org/10.25225/jvb.22062

Luo T, Yang Q, Wu L, Wang YL, Zhou JJ, Deng HQ, Xiao N, Zhou J (2023a) Phylogenetic relationships of Nemacheilidae cavefish (*Heminoemacheilus*, *Oreonectes*, *Yunnanilus*, *Paranemachilus*, and *Troglonectes*) revealed by analysis of mitochondrial genome and seven nuclear genes. Zoological Research 44(4): 693–697. https://doi.org/10.24272/j.issn.2095-8137.2022.266

Luo T, Chen ZX, Zhao XR, Yu J, Lan CT, Zhou JJ, Xiao N, Zhou J (2023b) *Balitora anlongensis*, the first cavefish species of the genus *Balitora* (Teleostei, Balitoridae) from Guizhou Province, southwest China. ZooKeys 1185: 21–42. https://doi.org/10.3897/zookeys.1185.108545

Ma L, Zhao YH, Yang JX (2019) Cavefish of China. In: White WB, Culver DC, Pipan T (Eds) Encyclopedia of caves (3rd edn.). Academic Press, Pittsburgh, USA, 237–254. https://doi.org/10.1016/B978-0-12-814124-3.00027-3

Nguyen VH (2005) Freshwater fishes of Vietnam (Vol. II). Nha Xuat Ban Nong Nghiep, Hanoi, 760 pp. [In Vietnamese]

Nichols JT (1944) The Fresh-Water Fishes of China. Nature 154: 5. https://doi.org/10.1038/154005a0

Rainboth WJ, Kottelat M (1991) Indochinese nemacheilines: a revision of nemacheiline loaches (Pisces: Cypriniformes) of Thailand, Burma, Laos, Cambodia and southern Viet Nam. Copeia, 1991. https://doi.org/10.2307/1446613

Rambaut A (2018) Figtree ver 1.4.4. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh.

Ronquist F Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Sauvage HE (1874) Notices ichthyologiques. II. Sur un cyprin de genre nouveau provenant de Chine. Revue et Magasin de Zoologie 2(3): 332–340.

Shao WH, Cheng GY, Lu XL, Zhou JJ, Zeng ZX (2024) Description of a new troglobitic *Sinocyclocheilus* (Pisces, Cyprinidae) species from the upper Yangtze River Basin in Guizhou, South China. Zoosystematics and Evolution 100: 515–529. https://doi.org/10.3897/zse.100.119520

Shi C, Yao M, Lv X, Zhao Q, Peng Z, Luo Y (2018) Body and organ metabolic rates of a cave fish, *Triplophysa rosa*: influence of light and ontogenetic variation. Journal of comparative physiology. B, Biochemical, Systemic, and Environmental Physiology 188(6): 947–955. https://doi.org/10.1007/s00360-018-1178-x

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England) 30(9): 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Molecular Biology and Evolution 38(7): 3022–3027. https://doi.org/10.1093/molbev/msab120

Wang CB, He L (2024) First discovery of troglobitic Paederinae (Coleoptera, Staphylinidae) from China. ZooKeys 1216: 27–42. https://doi.org/10.3897/zookeys.1216.132155

Wu YF, Wu CZ (1992) The fishes of the Qinghai-Xizang Plateau. Sichuan Publishing House of Science and Technology, Chengdu, 599 pp. [In Chinese, English summary]

Wu TJ, Wei ML, Lan JH, Du LN (2018) *Triplophysa anshuiensis*, a new species of blind loach from the Xijiang River, China (Teleostei, Nemacheilidae). ZooKeys 744: 67–77. https://doi.org/10.3897/zookeys.744.21742

Xiong KY, Sun ZY, Guo YS (2017) Revision of *Homatula* and *Schistura* classification in Sichuan Province. Journal of China Southwest Normal University 38(1): 21–27. [Natural Sciences] [In Chinese, English abstract] https://link.cnki.net/doi/10.16246/j.issn.1673-5072.2017.01.004

Yan YL (2017) The origin and evolution of cave-dwelling group of *Triplophysa* fishes (Teleostei, Cypriniformes, Nemacheilidae). (Doctoral dissertation, Southwest University). [In Chinese, English abstract]

Yang GY, Yuan FX, Liao YM (1986) A new blind Cobitidae fish from the subterranean water in Xiangxi, China. Huazhong Nongye Daxue Xuebao 5(3): 219–223. [In Chinese]

Yang W, He L, Yu H, Lin Y (2023) A new cave-dwelling spider of the genus *Speleoticus* (Araneae, Nesticidae) from Sichuan, China. Biodiversity Data Journal 11: e107751. https://doi.org/10.3897/BDJ.11.e107751

Zhang CG, Zhao YH (2016) Species Diversity and Distribution of Inland Fishes in China. Science Press, Beijing, 127–151. [in Chinese]

Zhang CG, Zhao YH, Yang, JX (2019) Fishes in the Jinsha Jiang River Basin, the Upper Reaches of the Yangtze River, China [M]. Science Press, Beijing. [in Chinese]

Zhang CY, Luo P, Huang F, Zhang E (2024) Revision of the loach genus *Claea* Kottelat, 2010 (Teleostei: Nemacheilidae) in China, with a description of a new species from the Chang-Jiang basin. Zootaxa 5543(3): 404–422. https://doi.org/10.11646/zootaxa.5543.3.6

Zhang J, Shu L, Peng Z (2024) Adaptive evolution of mitochondrial genomes in *Triplophysa* cavefishes. Gene 893: 147947. https://doi.org/10.1016/j.gene.2023.147947

Zhao YH, Zhang CG (2009) Endemic fishes of *Sinocyclocheilus* (Cypriniformes: Cyprinidae) in China species diversity, cave adaptation, systematics and zoogeography. Science Press, Beijing. [In Chinese]

Zhu SQ (1989) The loaches of the subfamily Nemacheilinae in China (Cypriniformes: Cobitidae). Jiangsu Science and Technology Publishing House, Nanjing, 150 pp. [In Chinese, English summary].

Zhu SQ, Cao WX (1988) Descriptions of two new species and a new subspecies of Nemacheilinae from Yunnan Province (Cypriniformes: Cobitidae). Acta Zootaxonomica Sinica 13(1): 95–100. [In Chinese, English summary]

Supplementary material 1

Raw data of the type speciemens of *Claea scet*

Authors: Hao-Tian Lei, Li He, Jun-Hao Huang, Jia-Jun Zhou, De-Kui He

Data type: xlsx

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